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The Mathematical Analysis of Life History Evolution In Plants.

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1. INTRODUCTION

Leslie matrix model has been developed as the useful tool for the demographic analysis of animal populations with age-specific reproduction and survival (Lewis 1942, Leslie 1945). However, the model is inadequate for plant populations because the reproduction and survival of plants depend on mainly their stage and/or size rather than their age. Thus Lefkovitch (1965) expanded Leslie matrix model in order to describe the dynamics of the population with stage-specific reproduction and survival. Thus, many authors (Sarukhan and Gadgil 1974, Bierzychudek 1982, Kawano et al. 1988) employed Lefkovitch matrix model in order to analyze the demography of perennial plant populations.

On the other hand, Leslie matrix model is recently reconsidered among mathematical ecologists as a new tool to analyze the evolution of life history of species. This is because elements of the matrices can be considered as life history parameters and fitness can be calculated on the basis of them. Charlesworth(1980) discussed, in his book, the evolution of senescence and of the timing of reproduction in age-structured populations, using the Leslie matrix model. Caswell(1982b) also used Leslie matrix model and concluded that survival costs should vary with age and that fertility costs should vary as the slope of the stable age distribution. However, their analytical method cannot be directly applied to the study of the evolution of the life history in perennial plants because their method was restricted in the cases with (i) age-structured population and (ii) density-independent dynamics.

As mentioned above, perennial plants show the size-dependent life history due to their plasticity. For example, most of perennial plants reproduce sexually when the size of individuals exceeds a threshold and many ageing seedlings of trees may be found far beneath the tree canopy (Oskar syndrome; Silvertown 1987) and so on. Moreover, the behavior of perennial plants is strongly affected

by the population density due to their immobility. Some authors suggested that the density-dependency of seedling mortality is much significant for the dynamics of perennial plant population (Solbrig et al. 1988). Thus the evolution of the life history in perennial plants will be also affected by the density-dependency. Therefore, in order to examine the evolutionary significance of such a complicated life history, we need a new method being able to deal with the case with the stage-specific life history and density-dependent dynamics.

In the present paper, we will consider the evolution of the life history in the population with stage-structure and density-dependent dynamics. Here we use a density-dependent Lefkovitch matrix model.

2. Invadable condition

Let n_{it}, $\vec{n}_t = (n_{1t}, n_{2t}, \ldots, n_{st})^T$, N_t be the population density of stage-class i at time t, the stage-class vector at time t and the total population density at time t, respectively, where s is the number of stage-classes and

(1) $$N_t = \sum_{i=1}^{s} n_{it} .$$

Let $\mathbf{L}(N_t)$ be the nonnegative density-dependent Lefkovitch matrix, each of whose element, $l_{ij}(N_t)$, represents the transition probability from the stage-class j to i.

According to the knowledge of Lefkovitch matrix model (Lefkovitch 1965), the dynamics of population with stage-structure can be written as:

(2) $$\vec{n}_{t+1} = \mathbf{L}(N_t)\, \vec{n}_t \quad .$$

The dynamical system (2) may have the oscillatory behavior or chaotic behavior of the total density N_t (Guckenheimer et al. 1977, Allen 1989). However, we consider here only the situation such that the state of the system (2) can reach to an equilibrium of the total density. Let $n_i^* > 0$, $\vec{n}^* = (n_1^*, n_2^*, \ldots, n_s^*)^T$, N^* be the population density of stage-class i at the equilibrium, the stage-class vector at the equilibrium and the total population density at the equilibrium, respectively. From Eq. (1), we obtain

(3) $$N^* = \sum_{i=1}^{s} n_i^* \quad .$$

At the equilibrium,

(4) $$\vec{n}^* = \mathbf{L}(N^*)\, \vec{n}^* \quad ,$$

is satisfied. Note that the Lefkovitch matrix at the equilibrium, $\mathbf{L}(N^*)$, has an eigenvalue 1 and $\vec{n}^*$ is its right eigenvector from Eq. (4). Thus N^* satisfies the equation

(5) $\det[\mathbf{L}(N^*) - \mathbf{I}] = 0$.

From Frobenius theorem (Gantmacher 1960), if $\vec{n}^*$ is a nonnegative eigenvector then the corresponding eigenvalue(i. e. 1) is the dominant eigenvalue.

Suppose that a population at a certain habitat is composed of individuals with the same life history characteristics (we refer those individuals to wild-type) and that the population is at the equilibrium state (Fig. 1). Then a small number of individuals with different life history characteristics from wild-type (we refer those individuals to mutant-type) happened to invade the habitat. We discuss about what kind of mutant-type could succeed in invading there. Let $\mathbf{L}(N_t)$ and $\mathbf{L}'(N_t)$ be a Lefkovitch matrix describing the life history parameters of wild-type and mutant-type, respectively. We assume that $\mathbf{L}(N_t)$ and $\mathbf{L}'(N_t)$ is irreducible. The irreducibility means that an individual at any stage has the possibility that the individual reaches an arbitrary stage after several steps. We also assume that $\mathbf{L}'(N_t)$ differs from $\mathbf{L}(N_t)$ slightly, i.e. only the small changes in life history parameters occur by mutation. Thus $l'_{ij}(N_t)$ is written by $l'_{ij}(N_t)=l_{ij}(N_t)+\delta l_{ij}(N_t)$. Furthermore, it is assumed, for simplicity, that a mutant-type individual gives the same density effect on others as a wild-type individual and vice versa.

The dynamics of the system containing two-type individuals is:

$$\begin{cases} (6\text{-}1)\ \vec{n}_{t+1} = \mathbf{L}(N_t+\delta N_t)\ \vec{n}_t \\ (6\text{-}2)\ \vec{\delta n}_{t+1} = \mathbf{L}'(N_t+\delta N_t)\ \vec{\delta n}_t , \end{cases}$$

where $\vec{\delta n}_t = (\delta n_{1t}, \ldots, \delta n_{st})^T$ is a stage-class vector of mutant-type individuals, i. e.

$$\delta N_t = \sum_{i=1}^{s} \delta n_{it} .$$

From Eq. (6-2), we obtain approximately as

$$\vec{\delta n}_{t+1} \cong \mathbf{L}'(N^*)\ \vec{\delta n}_t + \frac{d\mathbf{L}'(N^*)}{dN^*}\{\delta N_t+(N_t-N^*)\}\ \vec{\delta n}_t$$

$$(7) \qquad \cong \mathbf{L}'(N^*)\ \vec{\delta n}_t ,$$

because $N_t - N^*$ is sufficiently small at the invasion phase, where

$$\frac{d\mathbf{L}'(N^*)}{dN^*} = \begin{pmatrix} \frac{dl'_{11}(N^*)}{dN^*} & \cdots & \frac{dl'_{1s}(N^*)}{dN^*} \\ \vdots & \ddots & \vdots \\ \frac{dl'_{s1}(N^*)}{dN^*} & \cdots & \frac{dl'_{ss}(N^*)}{dN^*} \end{pmatrix}.$$

From Eq.(7), the mutant-type individuals are invadable, when the dominant eigenvalue of $\mathbf{L}'(N^*)$ is larger than 1.

Result 1 *The sufficient condition such that a mutant-type can invade the wild-type population is*

(8) $\boldsymbol{v}^T \boldsymbol{\delta L}(N^*)\boldsymbol{u} > 0$,

where $\boldsymbol{u}$, $\boldsymbol{v}^T$ *are the right and left eigenvectors of* $\boldsymbol{L}(N^*)$ *corresponding to the eigenvalue 1, respectively, satisfying the normalization condition* $\boldsymbol{v}^T\boldsymbol{u} = 1$ *and* $\boldsymbol{\delta L}(N^*)$ *is the matrix whose elements are* $\delta l_{ij}(N^*)$. *The necessary condition for the invasion of a mutant-type is*

(9) $\boldsymbol{v}^T \boldsymbol{\delta L}(N^*)\boldsymbol{u} \geq 0$

3. Meaning of the invadable condition

Suppose that a mutant-type can invade the wild-type population and that the the mutant-type can drive out all of the previous wild-type individuals (Fig. 2). At the new equilibrium, the mutant-type population has another steady-state density, N**. The steady-state population density satisfies the equations like Eq. (5):

(10) $\det [\mathbf{L}'(N^{**}) - \mathbf{I}] = 0.$

Since only the small changes in life history parameters occur by mutation, N** can be written as N* + δN*. The increment of the population density, δN*, is obtained as

$$(11) \qquad \mathbf{v}^T \boldsymbol{\delta L}(N^*)\mathbf{u} = -\mathbf{v}^T \left\{ \delta N^* \frac{d\mathbf{L}(N^*)}{dN^*} \right\} \mathbf{u} ,$$

$$(12) \qquad \delta N^* = \frac{\mathbf{v}^T \delta \mathbf{L}(N^*)\mathbf{u}}{-\mathbf{v}^T \frac{d\mathbf{L}(N^*)}{dN^*}\mathbf{u}} ,$$

where

$$\frac{dL(N^*)}{dN^*} = \begin{pmatrix} \frac{dl_{11}(N^*)}{dN^*} & \cdots & \frac{dl_{1s}(N^*)}{dN^*} \\ \vdots & \ddots & \vdots \\ \frac{dl_{s1}(N^*)}{dN^*} & \cdots & \frac{dl_{ss}(N^*)}{dN^*} \end{pmatrix}.$$

The left-hand side of Eq.(11) represents the increase of the population growth rate ($\delta\lambda$ in Eq.(8)) due to the changes in life history parameters ($\delta L(N^*)$). The right-hand side represents the decrease of the population growth rate due to the increase of the population density (δN^*). When these two terms balance, the dynamics is at the new equilibrium. The following result is derived from Eq.(12).

Result 2 *If* $\frac{dL(N^*)}{dN^*} \leq 0$ *for all i,j and* $\frac{dL(N^*)}{dN^*} < 0$ *for at least one set of (i,j), then the invadable condition is equivalent with the condition of* $dN^* > 0$.

In other words, if the density-dependency only operates negatively for all the entries of Lefkovitch matrix, then the equilibrium density of the invadable mutant-type (N**) is larger than that of the wild-type (N*). In this case, K- selection acts even on the stage-structured population.

4. Evolution of perennial plants with vegetative reproduction.

In this section, we show an example to analyze the life-history evolution in perennial plants using the above results. In the example, it is assumed that the hypothetical perennial plant has three stages (i.e. the seedling stage(S), the immature stage(juvenile: J) and the mature stage(flowering: F)) and that the population can always reach the new equilibrium composed of only mutant-type individuals after each successful invasion.

The Lefkovitch matrix of the hypothetical perennial plants with vegetative reproduction is

	S	**J**	**F**
Seedling	0	0	$fS_0(N)$
Juvenile	S_{JS}	S_{JJ}	V
Flowering	0	S_{FJ}	S_{FF}

,

where S_{ij} represents the transition probability from the stage j to i, f is the number of seeds per plant , $S_0(N)$ represents the germination rate of seeds ($0 \leq S_0(N) \leq 1$) and V represents the average number of vegetatives per flowering individual. When S_{FF} is zero, this matrix represents the life history of monocarpic perennial plants because individuals at the flowering stage always disappear next year.

There are three ways to reserve the parent's genes next year: seed production, vegetative reproduction and survival of flowering plants. The expected contribution by each way to the population differs because the probability of successful maturing is different in each way. For simplicity, we make the following assumptions:

(a) The perennial species regenerates by both the seed production and vegetative reproduction and only the flowering plants can reproduce vegetatives belonging to the juvenile stage. Thus

(13) $0 < S_{JS}, S_{JJ} + S_{FJ}, S_{FF} < 1$ and $V > 0$.

(b) Only the germination rate of seeds is density-dependent and a decreasing function of population density N , i. e. the derivative of $S_0(N)$ is negative.

(c) There is a trade-off between the seed number (f) and the survival rate of flowering individual (S_{FF}) because seed production causes the increase of the mortality risk of individuals due to much consumption of assimilating products (Fig. 3).

(d) The mutation occurs only along the trade-off curve ($f \equiv g(S_{FF})$ and $g' < 0$).

From Eq. (5), N * satisfies the following equation:

(14) $$S_{JS}S_{FJ}fS_0(N^*) = (1-S_{JJ})(1-S_{FF}) - VS_{FJ} > 0$$

because $S_0(N)$ is the positive function. The eigenvectors of $\mathbf{L}(N)$ corresponding to the eigenvalue = 1 are

(15) $$\mathbf{u} = \begin{bmatrix} (1-S_{JJ})(1-S_{FF}) - VS_{FJ} \\ (1-S_{FF})S_{JS} \\ S_{FJ}S_{JS} \end{bmatrix} > 0 , \mathbf{v} = \frac{1}{D}\begin{bmatrix} S_{JS} \\ 1 \\ \frac{1-S_{JJ}}{S_{FJ}} \end{bmatrix} > 0 ,$$

where $D = \{(1-S_{FF})(1-S_{JJ}) - VS_{FJ} + (1-S_{JJ}) + (1-S_{FF})\}S_{JS} > 0$ from Eqs. (13) and (14). Since only f and S_{FF} change due to mutation, $\delta\mathbf{L}(N^*)$ is

$$(16)\quad \delta \mathbf{L}(N^*) = \begin{bmatrix} 0 & 0 & S_0(N^*)\delta f \\ 0 & 0 & 0 \\ 0 & 0 & \delta S_{FF} \end{bmatrix}.$$

Thus we obtain the invadable condition from Eqs. (8), (14),(15) and(16) as:

$$(17)\quad \delta \left(\frac{f}{(1-\frac{VS_{FJ}}{1-S_{JJ}}) - S_{FF}} \right) > 0 .$$

Eq.(17) suggests that whether V=0 or not affects the results of evolution of plants' life history significantly. When V=0, Eq.(17) includes only two variables, f and S_{FF}. It also suggests that the results of evolution do not depend on the other variables, i. e. S_{JJ} and S_{FJ}. Since S_{JJ} and S_{FJ} depend on the survival rate and the growth rate at juvenile stage, i. e. the environment at younger stages, the results in this case are irrespective of the environment at younger stages and depend only on the shape of the trade-off curve ($f=g(S_{FF})$).

In contrast with the previous case, when $V \neq 0$, the results depend on V, S_{JJ} and S_{FJ}. It implies that our result depends on the survival rate and the growth rate at juvenile stage, i. e. the environment at younger stages. However, our result is independent of the germination rate of seedlings, $S_0(N)$.

The value of $\dfrac{f}{(1-\frac{VS_{FJ}}{1-S_{JJ}}) - S_{FF}}$ has the maximum at ESS because $\dfrac{f}{(1-\frac{VS_{FJ}}{1-S_{JJ}}) - S_{FF}}$ increases in the course of evolution (Eq.(17), Fig, 3). Thus, the slope of the line drawn from $(1 - \frac{VS_{FJ}}{1-S_{JJ}}, 0)$ to a point on the trade-off curve is minimum at the ESS point (S_{FF}^*, f *). The results in both cases (V=0 and $V \neq 0$) are summarized as follows:

(I) No vegetative reproduction(V=0)

When the trade-off curve is concave as shown in Fig. 4a, (0, g(0)) is ESS. In this case, monocarpic perennial plants are favored.

When the trade-off curve is convex, there are two cases.

Case(1) If $g'(0) \leq -g(0)$, then (S_{FF}^*, f^*) is $(0, g(0))$. It means that, if one produced seed needs much cost, monocarpic perennial plants are favored (Fig. 4b).
Case(2) If $g'(0) > -g(0)$, then the interior ESS is favored. It means that polycarpic perennial plants are favored in this case (Fig. 4c).
(II) With vegetative reproduction($V \neq 0$)

When the trade-off curve is concave as shown in Fig. 5a, $(0, g(0))$ is ESS. In this case, monocarpic perennial plants are favored.

When the trade-off curve is convex, there are three cases as shown in Fig. 5b, 5c and 5d.

Case(1) If $g'(0) \leq -\dfrac{g(0)}{1-\dfrac{VS_{FJ}}{1-S_{JJ}}}$ and $S_{FFmax} < 1-\dfrac{VS_{FJ}}{1-S_{JJ}}$, then (S_{FF}^*, f^*) is $(0, g(0))$. It means that if one produced seed needs much cost, then monocarpic perennial plants are favored (Fig. 5b).

Case(2) If $g'(0) > -\dfrac{g(0)}{1-\dfrac{VS_{FJ}}{1-S_{JJ}}}$ and $S_{FFmax} < 1-\dfrac{VS_{FJ}}{1-S_{JJ}}$, then the interior ESS is favored, i. e. polycarpic perennial plants are favored in this case. (Fig. 5c). If the environmrnt at juvenile stage is deleterious, i. e. S_{FJ} and S_{JJ} are low, there is a high posibility that monocarpic perennial plants are favoured.

Case(3) If $S_{FFmax} > 1-\dfrac{VS_{FJ}}{1-S_{JJ}}$, then the strategy set of (S_{FF}, f) changes toward the point of $\left(1-\dfrac{VS_{FJ}}{1-S_{JJ}},\ g\left(1-\dfrac{VS_{FJ}}{1-S_{JJ}}\right)\right)$ by the successive mutant invasion (Fig. 5d). If $S_{FF} > 1-\dfrac{VS_{FJ}}{1-S_{JJ}}$, then the dynamical system based on the matrix in the example has no equilibrium because the right-hand side of Eq.(14) is negative from the positivity of $S_0(N)$ and the above inequality. Since we have assumed that the system of Eq. (2) has an equilibrium, we cannot apply our results to the cases where $1-\dfrac{VS_{FJ}}{1-S_{JJ}} \leq S_{FF}$. In order to examine the invadability of the mutant-type with $S_{FF} > 1-\dfrac{VS_{FJ}}{1-S_{JJ}}$, it is necessary to make a computer simulation model which describes the invasion process of Eq. (6).

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Fig. 1

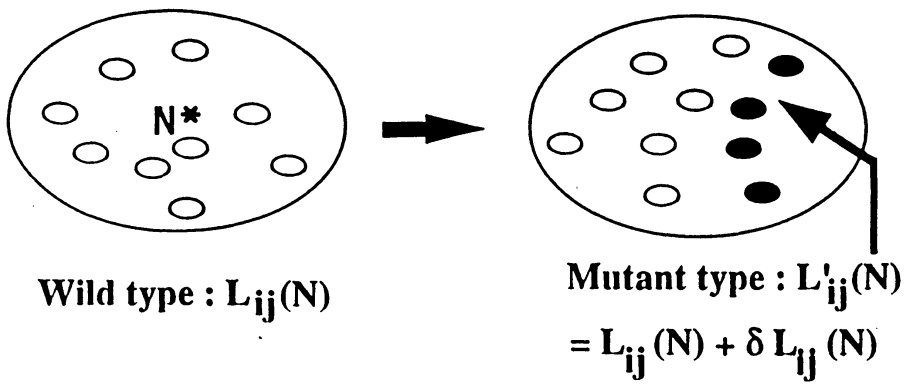


Fig. 2

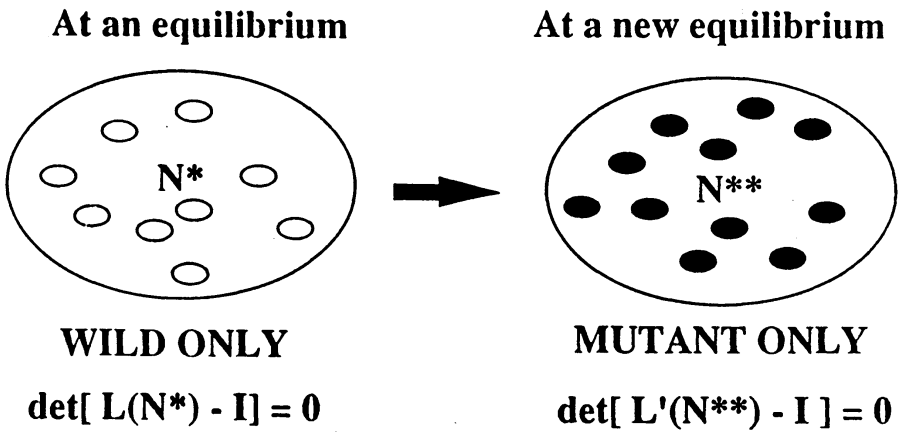


Fig. 3

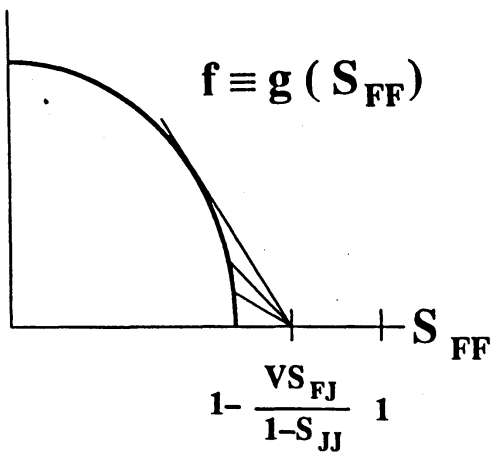


Fig. 4

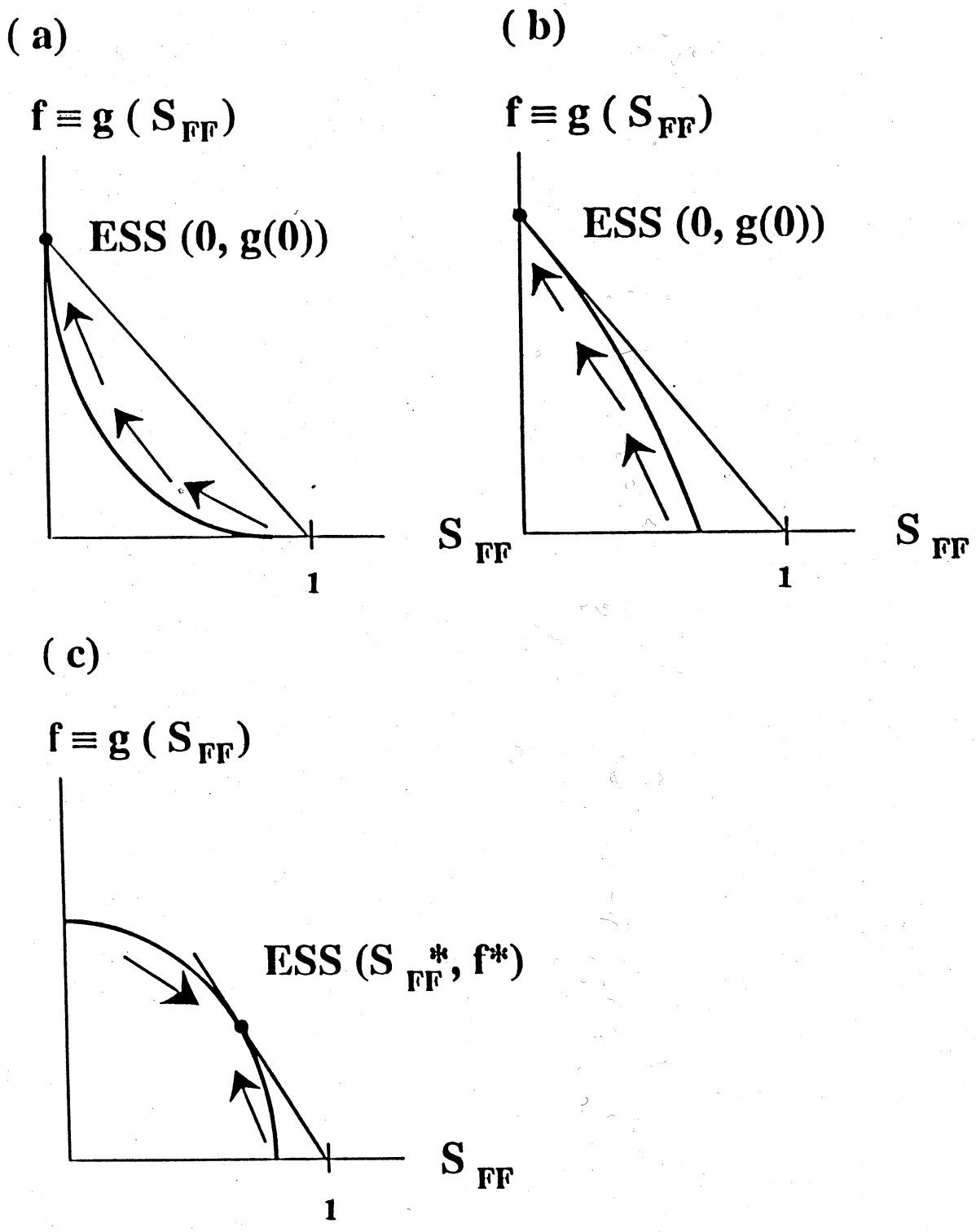
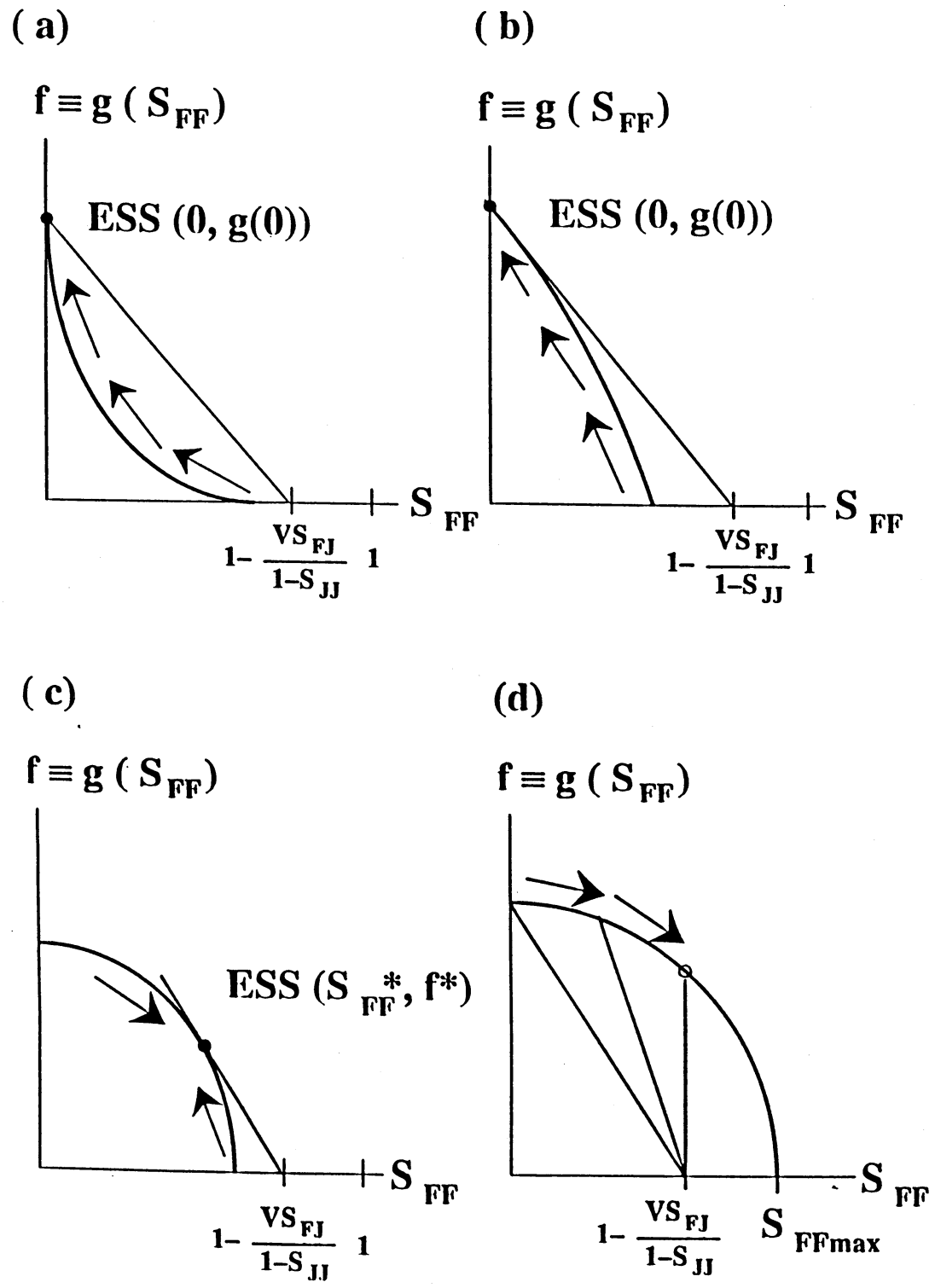


Fig.5


(a)
f ≡ g (S FF)
ESS (0, g(0))
S FF
1- VS FJ / 1-S JJ 1
(b)
f ≡ g (S FF)
ESS (0, g(0))
S FF
1- VS FJ / 1-S JJ 1
(c)
f ≡ g (S FF)
ESS (S FF*, f*)
S FF
1- VS FJ / 1-S JJ 1
(d)
f ≡ g (S FF)
S FF
1- VS FJ / 1-S JJ
S FFmax